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POPULATION ECOLOGY AND DEMOGRAPHY OF AN ENDEMIC SUBALPINE CONIFER (*PINUS BALFOURIANA*) WITH A DISJUNCT DISTRIBUTION IN CALIFORNIA

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ABSTRACT

Foxtail pine, *Pinus balfouriana* Grev. & Balf., is an endemic subalpine conifer of California with two allopatric subspecies. The northern subspecies grows in northwestern California and the southern subspecies is found in the southern Sierra Nevada. We studied three northern and three southern populations of *P. balfouriana* to evaluate the population biology, demography, mortality agents, and environmental conditions in these contrasting regions. Northern populations exist under a mesic climatic regime, a diversity of geological substrates, stands of high tree species richness, lower densities and basal areas, but higher numbers of recruitment, with a relatively mixed size class distribution. Southern foxtail pine populations exist under a xeric climatic regime dominated by granitic substrates, with moderate to high stand densities, less tree species-rich, lower recruitment numbers, but higher basal areas; due to a skewed size class distribution with high representation of large diameter trees. Recruitment in the north averaged 169.3 seedlings/saplings ha^{-1}, compared to 91.3 seedlings/saplings ha^{-1} in the south, despite the fact that northern populations produce less cones on average (3695 cones ha^{-1}) than populations in the southern Sierra Nevada (7642 cones ha^{-1}). At the stand-level, solar radiation input and foxtail pine density were correlated with fecundity. These factors may correspond with microenvironmental and topographic conditions that favor germination (e.g., warmer microclimate) and propagule pressure (e.g., seed supply). At the local or plot-level, microenvironmental conditions (e.g., litter, substrate type, and microhabitat) and factors corresponding to local seed supply (e.g., density, basal area, number of cones, and number of reproductive adults) were correlated with recruitment, particularly in the southern Sierra Nevada. Foxtail pine is recruiting episodically in higher numbers in the north and lower numbers in the south. Four of six populations appear to be stable, due to low mortality and high survivorship. Low estimates of population growth (λ) at Lake Mountain (north) and Sirretta Peak (south) were due to mortality of large diameter trees and low recruitment. At these locations, mountain pine beetle-mediated mortality and drought stress appear to be important factors contributing to current population trends.

Key Words: *Cronartium ribicola*, demography, endemic conifer, Foxtail pine, *Pinus balfouriana*, population structure, recruitment, subalpine.

Species and ecosystems at high latitudes and elevations are considered to be the most sensitive to global climate change (Parmesan 2006). A recent bioclimatic model has predicted significant range contractions for an important subalpine conifer (whitebark pine, *Pinus albicaulis* Engelm.) in western North America (Rehfeldt et al. 2006). This model and others like it, that project species distributions, are based on climate variables and species abundance (e.g., Lenihan et al. 2003; Rehfeldt et al. 2006; Beaumont et al. 2007). However, these models lack key information on population dynamics (e.g., fecundity, survival, mortality, and growth), dispersal, biotic interactions (e.g., competition, disease, and insects), genetics, and environmental heterogeneity. Clark et al. (2011) highlight the importance of incorporating demographic parameters (fecundity, mortality, survival, growth) in evaluating species responses to climate change. With that said, field-based ecological and demographic approaches are necessary to understand basic population biology and in turn the potential vulnerability of forest tree species to natural and anthropogenic disturbances.

Non-native pathogens, climate change, and climate-driven outbreaks of native insects are three threats to high elevation white pines in western North America (Tomback and Achuff 2010). Foxtail pine (*Pinus balfouriana* Grev. & Balf. subsp. *balfouriana*) is a high elevation white pine endemic to California, with two allopatric subspecies that are separated by approximately 500 km; one in the Klamath, Scott, and Yolla Bolly Mountains of northwestern California and the other in the southern Sierra Nevada (Mastrogiuseppe and Mastrogiuseppe 1980; Oline et al. 2000; see Fig. 1). For some time, the range disjunction was thought to have occurred during the Holocene Xerotherm (4000–8000 years ago; Axelrod 1976, 1977). Using a contemporary molecular genetic approach, Eckert et al. (2008) propose that this range disjunction occurred much earlier; in the Middle (0.13–0.86 million

FIG. 1. Location of study areas and foxtail pine distribution in California. *Pinus balfouriana* distribution map source: Little (1999).

years ago [Ma]) to Early Pleistocene (0.93–2.45 Ma). This time period corresponds with the Sherwin glaciation (~1 Ma) in the Sierra Nevada, one of the largest glacial episodes during the Pleistocene (Hill 2006; Eckert et al. 2008).

Geographic and temporal separation of the two subspecies corresponds with significant genetic, morphological, biochemical, and environmental differences (Bailey 1970; Snajberk et al. 1979; Mastrogiuseppe and Mastrogiuseppe 1980; Oline et al. 2000; Eckert et al. 2008; Eckert et al. 2010); potentially influencing the population biology and demography of foxtail pine in the two regions. For example, the northern subspecies (*P. b. balfouriana*) grows between 2050 and 2600 m, generally on the highest peaks and ridges, and separated by deep valleys (Oline et al. 2000; Eckert et al. 2010). The "mountain island" nature of foxtail pine populations in the north results in little gene flow and large genetic diversity among stands (Oline et al. 2000; Eckert et al. 2010). Foxtail pine is often a dominant component in these stands but mixes with a diversity of subalpine conifer species such as red fir (*Abies magnifica* A. Murr.), mountain hemlock (*Tsuga mertensiana* [Bong]. Carrière), lodgepole (*P. contorta* Douglas ex Loudon), whitebark (*P. albicaulis*), western white (*P. monticola* Douglas ex D. Don), and Jeffrey (*P. jeffreyi* Grev. & Balf.) pines (Oline et al. 2000; Eckert 2006). In this region the maximum attainable age for foxtail pine has been estimated to be between

1300–1500 years (Mastrogiuseppe and Mastrogiuseppe 1980). The southern subspecies (*P. b. austrina* R. J. Mastrog. & J. D. Mastrog.) in the southern Sierra Nevada grows between elevations of 2700 and 3600 m and defines timberline in this region. Here, stands are generally larger and more contiguous with less genetic differences among them, relative to differences within stands (Oline et al. 2000). In the south, foxtail may grow in pure stands or in association with species such as lodgepole, limber (*P. flexilis* E. James), or whitebark pine. Maximum attainable age for foxtail pine in the southern Sierra Nevada has been estimated to be between 2500–3000 years (Mastrogiuseppe and Mastrogiuseppe 1980).

Mountain climates throughout the range of foxtail pine are largely dominated by the California Mediterranean climatic regime, characterized by cold, wet winters, with long, warm, and dry summers. Within the Mediterranean climatic parameters, precipitation totals and growing season lengths vary considerably. The mountains of interior northwestern California receive high amounts of rainfall (≥1000–1500 mm) compared to the southern Sierra Nevada (<1000 mm). January minimum and July maximum temperatures differ considerably between the two regions as well, with warmer temperatures and longer growing seasons in the north compared to the south. In the north, foxtail occurs on a diversity of geological substrates and in the southern Sierra Nevada foxtail pine almost exclusively grows on granitic substrates (USDA, NRCS 2008).

Historical stand dynamics (e.g., mortality and recruitment) have been inferred from dendrochronological studies of foxtail pine in the southern Sierra Nevada (Lloyd 1997; Lloyd and Graumlich 1997). These studies have shown that treeline populations of foxtail pine have fluctuated in elevation in response to changes in both temperature and precipitation (Scuderi 1987; Lloyd 1997; Lloyd and Graumlich 1997). In the Klamath Mountains environmental heterogeneity (e.g., substrate type, microsite conditions, topography, and species composition) can strongly influence not only the persistence of foxtail pine but also recruitment success and subsequent downslope expansion (Eckert 2006; Eckert and Eckert 2007). In a recent study Crimmins et al. (2011) report downhill shifts in numerous plant species in California; largely tracking climatic water balance rather than temperature. In the southern Sierra Nevada, recruitment success appears to be influenced by soil moisture and topographic position (e.g., slopes with higher radiant input), with recruitment patterns being episodic (Bunn et al. 2005).

Given autoecological and genetic differences between the two subspecies the objectives of the study were to determine: (*i*) population and stand characteristics of foxtail pine in the regions of the northern and southern subspecies, (*ii*) factors important to recruitment, and (*iii*) current structure and population trends. Knowledge of the population biology, demographics (e.g., survival, fecundity, and growth), and environment of foxtail pine populations in both regions is central to understanding how vulnerable this endemic conifer is to natural and anthropogenic disturbances (*Cronartium ribicola* J. C. Fisch.– cause of white pine blister rust [WPBR], outbreaks by the native insect *Dendroctonus ponderosae* Hopkins [mountain pine beetle, MPB], climate change, and fire) and how these might influence future populations of this narrowly distributed white pine.

Materials and Methods

Study Sites

During the summers of 2008–2009, we selected six study populations, with two or three permanent demographic plots per population (sampling area within a population = 4 ha), for a total of 16 plots on National Forest System lands in California (Fig. 1). Only two demographic plots were established at both North Yolla Bolly and Sirretta Peak due to small population sizes and logistics. Each of the six populations was located in a distinct watershed and distributed in the northern (three sites) and southern (three sites) regions to capture variation in the physical environment (e.g., climate, geology, topography, forest composition; see Fig. 1). Within the northern and southern subspecies distribution, study sites were located in the northern, central, and southern portions of foxtail pine's geographic range in each of those regions (Fig. 1). In northwestern California, study populations were located at Lake Mountain, Mount Eddy, and the North Yolla Bolly (listed from north to south). In the southern Sierra Nevada, study populations were located at Onion Valley, Cottonwood Pass, and Sirretta Peak (north to south, respectively).

Population and Stand Sampling

Once a population was located, a random starting point was chosen for the first plot; the second and third plots were sited ≥100 m from the first plot. Within a population, each of three replicate plots were 40 m × 100 m (4000 m^2) with sampling covering approximately 1.2 hectares within a 4-hectare area. The following data were recorded for each demographic plot: GPS location (UTM: NAD27 coordinates), slope (in percent), aspect, elevation (in meters), visible signs of past fire or ignition (i.e., basal fire scar, bole scorch, lightning strike), slope position (ridge-top, upper slope, mid-slope, lower slope,

valley bottom, or bench), and land-use history (e.g., historical logging, fire suppression, recent thinning, use of wildland fire, recreation, none), site condition (e.g., xeric or mesic), presence or absence of the Clark's nutcracker (*Nucifraga columbiana*). Clark's nutcracker is an important dispersal agent of many western pine species including the high elevation white pines such as whitebark pine, limber pine, and Great Basin bristlecone pine, *P. longaeva* D.K. Bailey (Lanner 1982, 1988; Tomback and Linhart 1990).

Within each demographic plot, all *P. balfouriana* were identified and diameter at breast height (d.b.h. in cm) recorded for all individual stems ≥1.37 m tall. Seedlings and saplings were all stems <1.37 m in height. All tree positions (x and y coordinates from the centerline of the plot) were recorded and mapped and data collected for tree status (live or dead), crown condition (rating 1–10 as follows: 1: ≤10% dead, dying, damaged, infected; 2: 11–20% dead, dying, damaged, infected; 3: 21–30% dead, dying, infected, etc.), and crown position (understory, suppressed, intermediate, codominant, dominant, or open). Signs and symptoms of pathogens (e.g., WPBR, dwarf mistletoe, and root diseases) and insects were also recorded. *Dendroctonus ponderosae* (MPB) was confirmed if there was the presence of pitch tubes, frass, and characteristic galleries (Furniss and Carolin 1977). Reproductive output was assessed by counting the number of current and previous years' cones per tree.

Seedlings and saplings <1.37 m tall were evaluated within each demographic plot by establishing three nested recruitment subplots that were 15 m × 15 m in size (totaling 225 m^2), for a total of nine regeneration plots/population (six regeneration plots for North Yolla Bolly and Sirretta Peak). All recruitment was counted and identified to species. For *P. balfouriana* recruitment, data were collected on basal diameter (cm), height (cm), crown condition, status (live or dead), disease condition, and whorls counted for aging. Microenvironmental conditions for each foxtail recruit were evaluated by measuring litter depth (cm), substrate type (e.g., exposed soil, decomposed granite, soil and litter, log, rock), canopy type (open/exposed, partially closed, and closed), and microhabitat condition (tree/shrub/log nurse, rock shelter, other, or none). A limited number of foxtail seedlings/saplings were sampled to obtain size-age relationships by counting growth rings, as well as measuring height, diameter, and number of whorls. We used a multiple linear regression to estimate age for recruitment present in demographic plots. Independent variables loaded into the regression model were height, whorl count, and diameter of field-sampled foxtails. Diameter explained 97% of the variation in the model and yielded parameter estimates and the regression equation $Y = 22.2949X_1 + 0.7683$; $r^2 = 0.971$ ($F_{1,6} = 169.19$, $P < 0.0001$). This equation was then used to estimate age and the year that a seedling or sapling had been recruited into a demographic plot.

A forest vegetation plot (40 m × 40 m) was nested within each demographic plot to obtain tree data for other tree species besides *P. balfouriana* (i.e., d.b.h., status, diseases, insects, crown condition, crown class, etc.). All tree and recruitment data at each plot were collected to quantify stand structure, composition, basal area, and density. Positions of all associate trees were recorded and mapped.

For each demographic plot, climatic parameters of mean, minimum, and maximum monthly and annual temperature and precipitation from the period of 1971–2000 were provided by FHTET (USDA FS Forest Health Technology Enterprise Team, Fort Collins, CO) using the PRISM climatic model (Daly et al. 1994). Parent material and soil survey data were provided by the South Lake Tahoe office of the USDA Natural Resources Conservation Service (NRCS). Percentage maximum solar radiation input was calculated using slope and aspect (Buffo et al. 1972).

A check of collinearity in the multiple linear regression model, to estimate recruitment age, was done employing leverage plots and bivariate scatterplots. Assumptions of normality and homogeneity of variances were checked and met. In addition we used a nonparametric test, Kendall's τ rank correlation, to determine if relationships exist between biological and environmental variables and foxtail pine recruitment for northern and southern populations. All statistical analyses were conducted with the software program JMP, version 8.0.1 (SAS Institute Inc. Cary, NC).

Current Population Trends

Population trends were assessed by employing transition matrix models for each of the six populations of foxtail pine. In our study, transition matrices are used to describe and summarize current trends in survivorship, mortality, fecundity, and to a much lesser extent growth, as this is a long-lived tree species. Transition matrix models of populations follow the Lefkovitch (1965) model:

$$n_{t+1} = An_t$$

where n_t is a column vector corresponding to the size structure at time t on the population classified into s size classes, and A is the matrix representing population dynamics. A is influenced by survival, growth, and reproduction. Entries in the transition matrix represent the

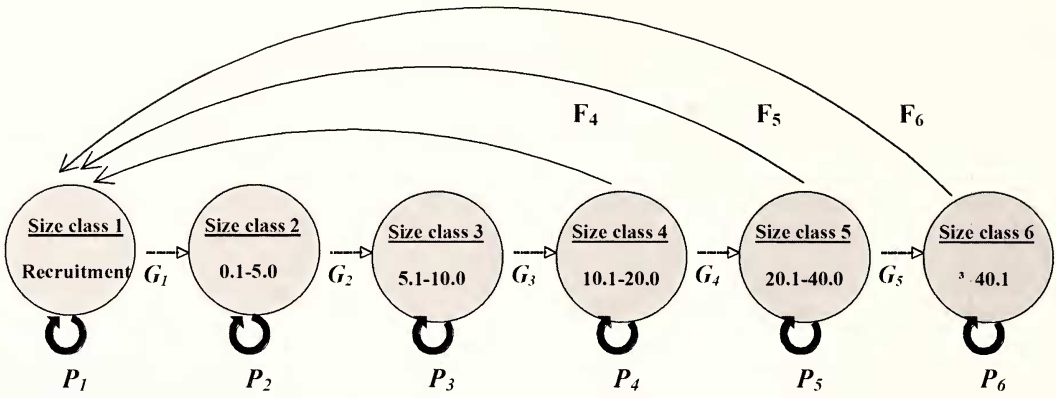


FIG. 2. Size-class transition model for foxtail pine populations in California. Size classes are represented by circles with size class 1 at the left and proceeding to size class 6 at the right. Transition probabilities for growth (G_1-G_5) are the forward horizontal arrows, survivorship (P_1-P_6) are the bold circular arrows, and fecundity (F_4-F_6) are the long arrows from right to left.

contribution each size class makes to every other size class during a specified time interval. We created sized-based models with six size classes: 1) recruits (individuals <1.37 m in height); 2) 0.1–5.0 d.b.h.; 3) 5.1–10 d.b.h.; 4) 10.1–20.0 d.b.h.; 5) 20.1–40.0 d.b.h.; and 6) ≥40.1 d.b.h. (Fig. 2). Transition probabilities were calculated and estimated from our field data. For growth probabilities, we assume that individuals will transition into the next size class if trees are in the upper d.b.h. limit of the size class, or height for seedlings/saplings. For example, an individual with a d.b.h. of 4.9 cm or 5.0 cm would grow into the next size class in the next time step. Where mortality occurred, survivorship was calculated using the number of standing dead trees (years dead ranged from 1–12 yr) divided by current live and dead stems for each size class. In demographic studies of forest trees where mortality was not observed, mortality was assumed to be 0% or 2% (Ettl and Cottone 2002; van Mantgem et al. 2004). In our populations where no mortality was observed, we assumed a minimal value of 1% mortality; an average of these previously published estimates. Fecundity was estimated from existing recruitment and cone production data we collected for size classes 4, 5, and 6. We used the following formula to estimate fecundity for each of the 3 size classes:

$$(\text{no. of cones in stage}(t)/\text{no. of cones for population}(t)) \times \frac{(\text{no. of recruits for population}(t))}{\text{no. of trees in stage}(t)}$$

where t is time. This formula is similar to that used by Davelos and Jarosz (2004) for estimating reproduction for American chestnut (*Castanea dentata* Marsh.).

The population growth rate (λ), as estimated using the dominant eigenvalue of the transition matrix (Caswell 2001), measures the rate of change in total population size. Population growth rate is a function of size- or age-specific rates of survival, growth and reproduction, with $\lambda > 1$ indicating growing, $\lambda = 1$ indicating stable, and $\lambda < 1$ indicating declining populations. Classical statistical tests using estimates of λ are inappropriate because demographic parameters and estimates of λ are not simple and their distributions are often not known (Caswell 2001). Therefore, we computed 95% confidence intervals for λ by bootstrapping (n = 10,000) across survivorship, growth, and fecundity estimates comprising the transition matrix. All calculations and bootstrapping were performed in Matlab (Mathworks Inc., Natick, MA). Kendall's τ rank correlation analysis was used to determine if relationships existed between biological and environmental variables and mean fecundity and survivorship. This nonparametric test was conducted with the software program JMP, version 8.0.1 (SAS Institute Inc. Cary, NC).

RESULTS

Forest and Stand Conditions

Locations ranged in elevation from 2086 to 3398 m, with stands varying in physiognomy and environmental characteristics (Table 1). Slopes ranged from 11 to 22 percent and aspect varied as well (Table 1). Demographic sites in the mountains of interior northwestern California receive high amounts of rainfall, ranging from 1051 mm to 1388 mm, compared to the southern Sierra Nevada with a range from 356 mm to 721 mm (Table 1). January minimum and July maximum temperatures also differ between the two regions, with warmer temperatures and relatively longer growing seasons in the north compared to the southern Sierra Nevada (Table 1). Relative humidity is on average higher in the north than in the south (61% vs. 44%; see Table 1). The percent

TABLE 1. CLIMATE AND GEOLOGY SUMMARIES FOR FOXTAIL PINE POPULATIONS. Climate averages for each population based on PRISM data for 30-year averages from 1970–2000 (Daly et al. 1994 and FHTET). Ann. ppt = total annual precipitation in millimeters (mm), average minimum temperature for January and average maximum temperature for July in degrees Celsius, GDD = growing-degree days, rel. humidity (%) = percent relative humidity, % max. rad. input (Cal. cm^{-2}/year) = percentage maximum solar radiation input was calculated using slope and aspect (Buffo et al. 1972). Soil data source: USDA NRCS (2008).

	Northern			Southern		
	Lake Mountain	Mount Eddy	North Yolla Bolly	Onion Valley	Cottonwood Pass	Sirretta Peak
Elevation (m)	2086	2453	2246	3073	3398	2925
Slope (%)	19	14	22	19	11	14
Aspect	133	135	208	27	207	250
Ann. ppt. (mm)	1313	1051	1388	356	439	721
Avg. min. temp. (°C)	−1.7	−3.1	−0.5	−1.7	−9.6	−5.5
Avg. max. temp. (°C)	24	29	26	29	16.7	21
May GDD	48	0	32	410	0	0
September GDD	323	83	191	131	0	145
Rel. humidity (%)	65	58	59	31	45	57
% max. rad. input (Cal. cm^{-2}/year)	85.39	92.36	95.89	54.42	90.61	85.02
Geology/parent material	gneiss/ metamorphic/ serpentine	serpentine/ metavolcanics	metamorphic	granitoid rock	subglacial till/granite	residuum weathered granite

maximum radiation input (Cal.cm^{-2}/yr) was higher in the northern foxtail stands, mean = 91.20, than in the southern Sierra Nevada, mean = 78.02 (Table 1). The geology of the Klamath region is very diverse and sites in the north span a range of geological substrates (gneiss, serpentine, metamorphic, and metavolcanics) versus the southern Sierra Nevada sites that are primarily on granite (Table 1).

White pine blister rust was only found in populations in the north, at Lake Mountain and Mount Eddy, with no rust in the Southern Sierra Nevada (Table 2). Mountain pine beetle was observed in 4 of the 6 sites with the highest incidence at Sirretta Peak followed by Lake Mountain (Table 2). Moderate mortality was found in 5 populations ranging from 0 to 14% with an average of 5.7% in the north and 9% in the southern Sierra Nevada (Table 2).

Clark's nutcracker was observed in 1 of 3 stands in the north and present in all 3 populations in the southern Sierra Nevada (Table 2). The only population in which Clark's nutcracker was observed in the north, at Mount Eddy, is also the only northern foxtail stand in which whitebark pine is an associate species. Whitebark pine is one of the preferred food resources for this corvid (Hutchins and Lanner 1982). Evidence of fire was found in 38% of the plots in the north and 88% in the southern Sierra Nevada (Table 2). In the southern Sierra Nevada, fire may be a relatively common disturbance agent in foxtail pine stands (Rourke 1988; North et al. 2009).

TABLE 2. BIOLOGICAL AND ENVIRONMENTAL SUMMARIES FOR FOXTAIL PINE POPULATIONS. P = presence and A = absence from stand.

	Northern			Southern		
	Lake Mountain	Mount Eddy	North Yolla Bolly	Onion Valley	Cottonwood Pass	Sirretta Peak
Pinus balfouriana density (inds. ha^{-1})	89	95	64	114	227	46
Pinus balfouriana basal area (m^2 ha^{-1})	10.6	26.4	10.8	27.3	43.2	13.4
Average *Pinus balfouriana* d.b.h.	27.9	45.2	35.3	44.1	35.9	50.9
Reproductive adults (inds. ha^{-1})	30	49	28	62	138	35
Cones (no. ha^{-1})	3966	3657	3463	7525	11,078	4325
Recruit. (inds.ha^{-1})	64	370	74	40	227	7
Clark's nutcracker	A	P	A	P	P	P
WPBR (%)	4	2	0	0	0	0
MPB (%)	4	2	0	1	0	16
Mortality (%)	13	4	0	6	7	14
Rock cover (%)	25.3	55.0	45.5	50.0	38.7	25.0
Evidence of fire (freq.)	33	50	33	100	66	100

Composition and Structure

Mean density of foxtail pine in northern stands was 82.6 trees/ha and ranged from 64 to 95 trees/ha (Table 2). In southern foxtail pine stands the mean density was 129 trees/ha and ranged from 46 to 227 trees/ha (Table 2). Mean basal area was higher in the southern stands, 27.9 m^2/ha, but ranged from 13.4 to 43.2 m^2/ha. Mean basal area in northern foxtail pine stands was 15.9 m^2/ha and ranged from 10.6 to 26.4 m^2/ha (Table 2). Relatively higher basal areas in southern foxtail pine stands corresponded with a larger average d.b.h. of 43.6 cm (range: 35.9 to 50.9), compared to the north, 36.1 cm (range: 27.9 to 45.2; Table 2). Foxtail pine is the dominant component in these stands with importance values ranging from a 56.4% to 100% (Table 3). Some common associates include red fir, western white pine, whitebark pine, limber pine and white fir (Table 3). Total tree density (all species) ranged from 67.3 to 227.0 individuals/ha and basal area ranged from 10.2 to a high of 43.2 m^2/ha (Table 3).

The size structure for northern populations is relatively mixed across diameter classes with the exception of Mount Eddy, which has higher numbers of trees in the largest size class (Fig. 3a). Size structure in the southern foxtail populations was generally skewed, with lower numbers in the smaller size classes and higher numbers in the largest size class (Fig. 3b). However, Cottonwood Pass has good representation of trees in the smallest size class (Fig. 3b).

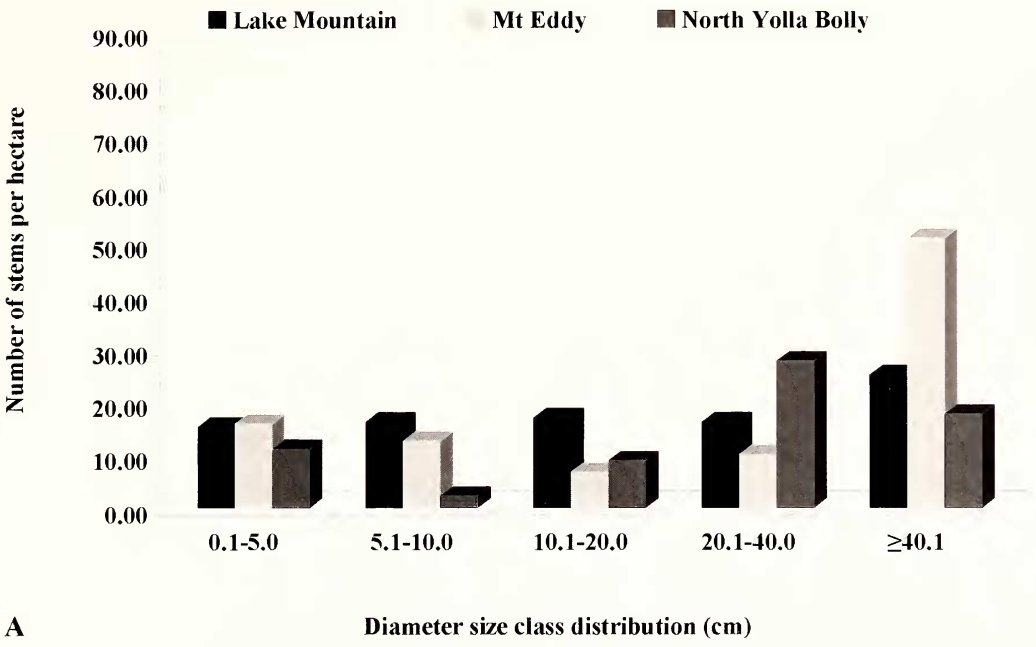
Reproductive Output and Recruitment Patterns

Southern foxtail stands had higher numbers of reproductive individuals, mean = 78.3, than northern stands, mean = 35.7 (Table 2). Higher numbers of reproductive adults corresponds with higher cone production in the south, mean = 7642 cones/ha, and in the northern populations cone production averaged 3695 cones/ha (Table 2). However, what appears to be somewhat higher reproductive output in the south does not correspond to higher numbers of seedlings and saplings. Regeneration in the north averaged 169.3 seedlings/saplings per hectare compared to 91.3 seedlings/saplings per hectare in the southern populations (Table 2).

Regional climate and landscape characteristics may strongly influence recruitment patterns, but microenvironmental conditions may be as influential in the successful establishment of foxtail pine as large-scale phenomena. Foxtail seedlings and saplings in the north were generally growing on microsites with low litter depths, on rocky substrates, and in open canopies (Table 4). In the southern foxtail pine stands, recruitment was growing more frequently on microsites with higher amounts of litter, decomposed granite, in

TABLE 3. STAND STRUCTURE AND COMPOSITION FOR SIX *PINUS BALFOURIANA* POPULATIONS. Relative density = RD, relative basal area = RBA, and importance value = IV of tree species ≥1.37 m. Importance values were calculated for each species as (relative density + relative basal area)/2.

Species	Northern									Southern								
	Lake Mountain			Mount Eddy			North Yolla Bolly			Onion Valley			Cottonwood Pass			Sirretta Peak		
	RD	RBA	IV %	RD	RBA	IV %	RD	RBA	IV %	RD	RBA	IV %	RD	RBA	IV %	RD	RBA	IV %
Abies concolor White fir	0.6	>0.5	0.3	—	—	—	—	—	—	—	—	—	—	—	—	1.5	>0.5	0.8
Abies magnifica Red fir	36.7	27.9	32.3	1.2	1.1	0.6	4.9	3.7	4.3	—	—	—	—	—	—	27.6	26.3	27.0
Pinus albicaulis Whitebark pine	—	—	—	16.1	3.8	10.0	—	—	—	21.4	5.5	13.5	—	—	—	—	—	—
Pinus balfouriana Foxtail pine	60.2	71.8	66.0	68.8	90.5	79.7	95.1	96.3	95.7	69.9	87.6	78.8	100	100	100	57.0	56.0	56.4
Pinus contorta Lodgepole pine	—	—	—	—	—	—	—	—	—	8.6	6.7	7.7	—	—	—	—	—	—
Pinus flexilis Limber pine	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3.0	3.5	3.3
Pinus monticola Western white pine	1.8	0.2	0.9	13.7	5.5	9.6	—	—	—	—	—	—	—	—	—	10.7	14.1	12.4
Pseudotsuga menziesii Douglas fir	0.6	>0.5	0.3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Total density (inds.ha^{-1})			148.2			139.1			67.3			163.3			227.0			81.25
Basal area (m^2 ha^{-1})			14.8			29.1			10.2			31.1			43.2			24.06



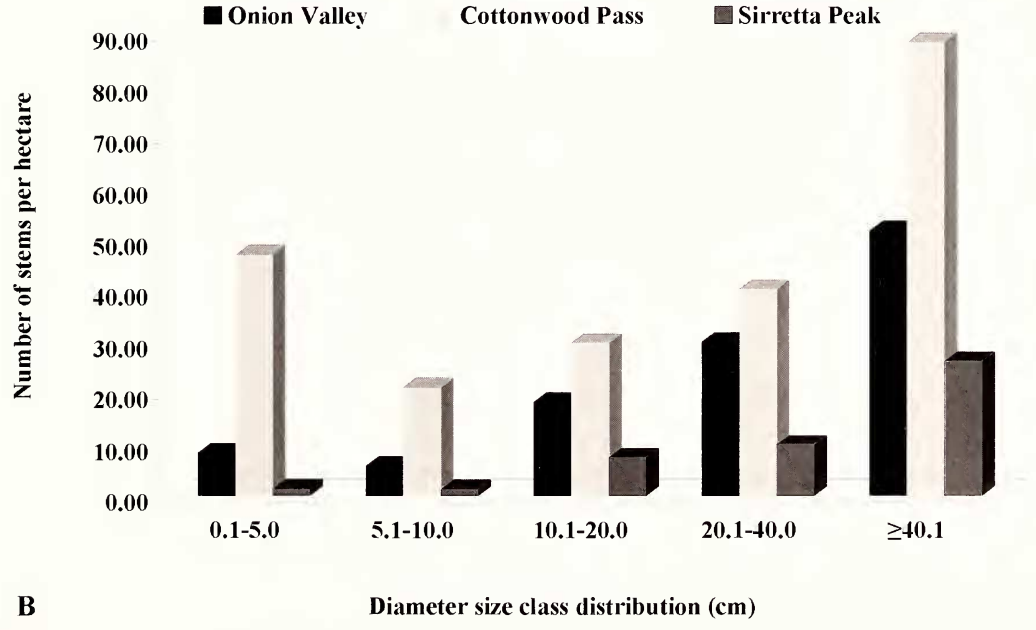


FIG. 3. Size structure of six foxtail pine populations from the northern (A) and southern (B) regions.

an open canopy, and associated with a rock shelter microhabitat (Table 4).

No relationships were found between biological and environmental variables and foxtail pine recruitment from demographic plots in the northern region (see Table 5). In the north the best relationship, albeit weak, was between recruitment and foxtail pine density (Table 5). Density of foxtail pine may correspond with dominance in a stand and possibly an increase in the source of propagules (e.g., seed) as well as a higher competitive advantage. Two of the three

TABLE 4. SUMMARY OF DOMINANT MICROENVIRONMENTAL CONDITIONS OF *P. BALFOURIANA* RECRUITMENT (INDIVIDUALS <1.37 MIN HEIGHT). Litter depth, in centimeters, surrounding seedling; substrate regeneration is growing in: es = exposed soil (no litter), dg = decomposed granite, sl = soil + litter, lg = log, rk = rock, or combinations dgl = decomposed granite + litter; canopy conditions: 1 = open/exposed, 2 = partially closed, 3 = closed; microhabitat conditions: 1 = tree/shrub nurse, 2 = rock shelter, 3 = other, 4 = none.

	Average recruitment ha^{-1}	Microenvironment			
		Litter depth (cm)	Substrate (freq.)	Canopy (freq.)	Microhabitat (freq.)
North	169.3	0.52	64 (rk)	94.8 (open)	86.7 (none)
South	91.3	2.40	54 (dgl)	83.3 (open)	78.1 (rock shelter)

study sites are located in areas with mixed geological sources including serpentine/ultramaphic substrate (see Table 1). If foxtail pine is dominant at a site with serpentine soils it may have a competitive advantage in recruiting more successfully than other conifer associates, particularly shade-intolerant species such as *Abies concolor* (Gordon & Glend.) Hildebr., *A. magnifica* and *Tsuga mertensiana* (Eckert and Eckert 2007; see also Table 3).

Strong positive relationships were found in the southern Sierra Nevada between foxtail recruitment and foxtail density, number of cones ha^{-1}, and number of reproductive adults; all corresponding with source strength and propagule pressure (Table 5). A strong negative relationship was found between recruitment and tree species richness (Table 5). In the southern Sierra Nevada foxtail pine is often the dominant species, but in tree species-rich subalpine forests it may be at a competitive disadvantage in successfully recruiting into limited and favorable microsites (see Tables 3 and 4).

Despite differences in factors potentially important to recruitment of foxtail pine in the north and south, establishment patterns of foxtail pine in both regions appear to be somewhat episodic (Fig. 4). In the north, Mount Eddy appears to be recruiting relatively consistently since 1970, with a pulse of recruitment from 1998 to present (Fig. 4A). Recruitment number and patterns for both Lake Mountain and the North Yolla Bolly are generally low and episodic (Fig. 4A) as is the case with the southern Sierra Nevada (Fig. 4B). Cottonwood Pass is the only population in the south that has had a recent pulse of recruitment from 1998 to present (Fig. 4B). Recruitment at Onion Valley is fairly low and episodic and recruitment is almost non-existent at Sirretta Peak, and any individual <1.37 m in height recruited prior to 1970 (Fig. 4B).

Current Population Trends

Foxtail pine populations varied in fecundity, survivorship, and growth (Table 6, Appendix 1). Fecundity was quite variable and this is reflected in the variation we found in cone production, number of reproductive adults, and the number of seedlings that successfully established in each of these populations (Tables 2 and 6). For both northern and southern foxtail pine populations, fecundity was positively correlated with solar radiation input and foxtail pine density (τ = 0.466, P = 0.188; τ = 0.466, P = 0.188, respectively). Survivorship varied, due to differential mortality between populations (Tables 2 and 6), with trees in the largest diameter class (≥40.1 cm dbh) having relatively lower survival rates. Low estimates of survivorship were found at Lake Mountain and Sirretta Peak (Table 6, Appendix 1). A negative correlation was found between foxtail survivorship and incidence of MPB (τ = −0.41, P = 0.251). Growth is the least

TABLE 5. KENDALL'S τ RANK CORRELATIONS BETWEEN BIOLOGICAL AND ENVIRONMENTAL VARIABLES AND FOXTAIL PINE RECRUITMENT FOR NORTHERN (N = 8 PLOTS) AND SOUTHERN POPULATIONS (N = 8 PLOTS).

Variable	Northern		Southern	
	τ	P-value	τ	P-value
Ann. ppt.	0.000	1.000	0.000	1.000
Max July temp.	0.178	0.584	−0.481	0.117
No. cones	−0.231	0.441	0.691	0.017
Solar radiation	−0.077	0.797	0.109	0.708
Tree species richness	0.136	0.675	−0.645	0.041
Pinus balfouriana density	0.353	0.244	0.764	0.008
Pinus balfouriana basal area	−0.077	0.797	0.545	0.061
No. reproductive adults	−0.196	0.517	0.618	0.034
Litter depth	−0.105	0.800	0.195	0.534
Rock cover	0.117	0.698	−0.109	0.708

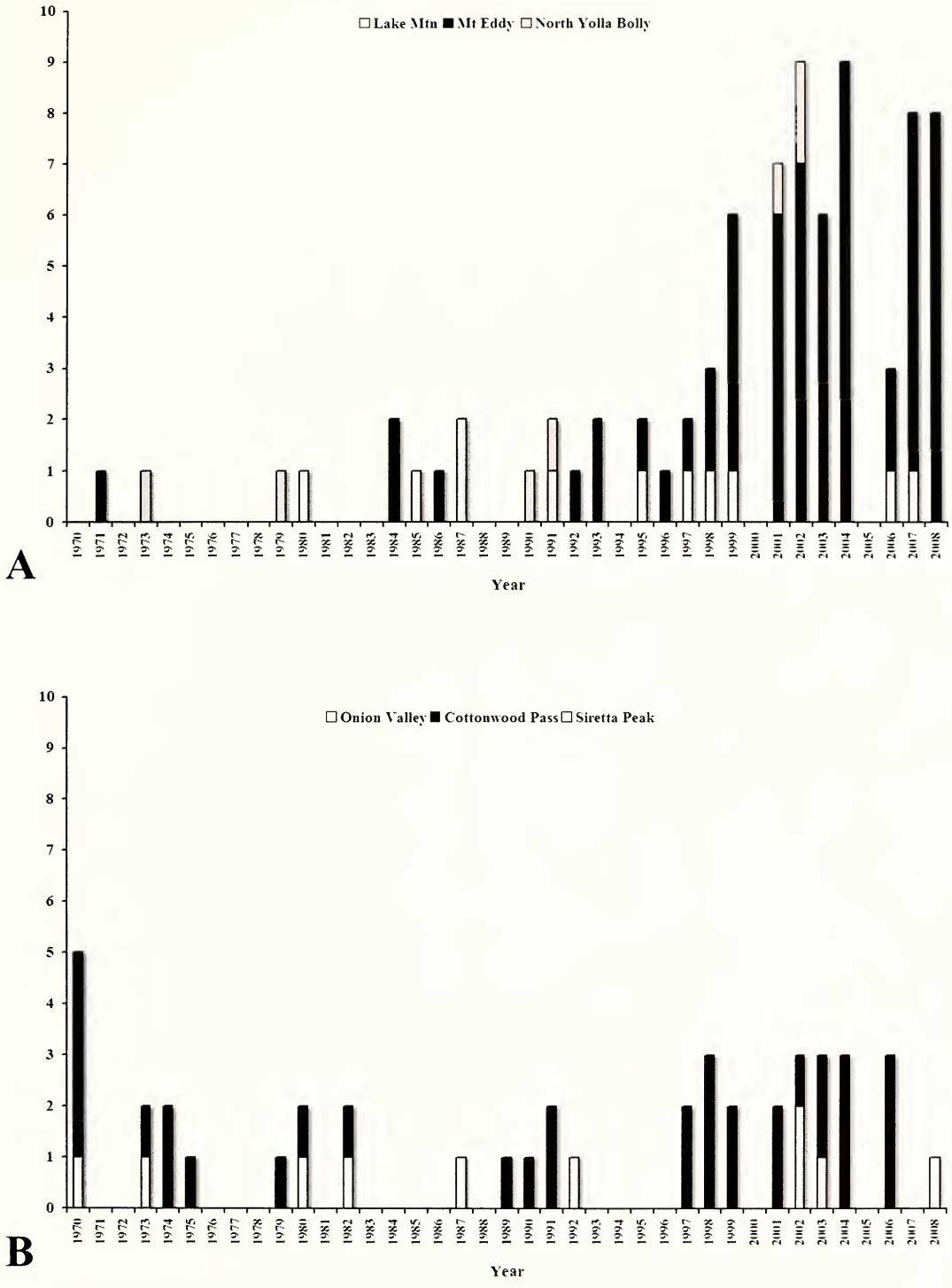


FIG. 4. Foxtail pine recruitment and establishment patterns for populations in the north (A) and south (B).

dynamic and variable transition element, given the long-lived nature of this tree species and a one-time sampling (Table 6, Appendix 1).

Estimates of population growth rate (λ) varied among foxtail sites, with 5 of the 6 having a $\lambda \geq 1.0$, indicating that most of these populations appear stable (Table 6). The North Yolla Bolly population had the highest λ, followed by Onion Valley, Mount Eddy, Cottonwood Pass, and Sirretta Peak (Table 6). Noteworthy of the North

TABLE 6. MEANS FOR ESTIMATED FECUNDITY, SURVIVORSHIP, AND GROWTH FROM SIZE-BASED TRANSITION MATRICES FOR SIX FOXTAIL PINE POPULATIONS. Estimated population growth rate, λ, is shown along with 2.5% and 97.5% confidence intervals (CI, in parentheses).

Population	Fecundity	Survival	Growth	λ (2.5%, 97.5% CI)
Lake Mountain	0.233	0.898	0.026	0.998 (0.588, 1.576)
Mount Eddy	0.677	0.971	0.012	1.013 (0.677, 1.552)
North Yolla Bolly	0.208	0.976	0.053	1.041 (0.703, 1.527)
Onion Valley	0.082	0.966	0.040	1.019 (0.775, 1.497)
Cottonwood Pass	0.242	0.950	0.025	1.011 (0.419, 1.720)
Sirretta Peak	0.026	0.906	0.066	1.007 (0.705, 1.571)

Yolla Bolly population is that it is the second smallest population with 141 individuals/ha (Sirretta Peak was the smallest with 54 individuals/ha), but it is the one population where no WPBR, MPB, or mortality was observed, with consistent and high survivorship across all size classes (Table 6, Appendix 1). Lake Mountain has a $\lambda < 1.0$, indicative of a population that may be in decline. At Lake Mountain both WPBR and MPB were present, with lower survivorship rates in size classes 3, 5, and 6 (Table 6, Appendix 1). All upper limit confidence intervals for λ were greater than 1, suggesting stability. However, for most populations the lower confidence interval was <1.0 (Table 6); whether this is cause for concern is difficult to assess, given that λ was estimated from a one-time sampling.

DISCUSSION

Ecological and environmental conditions clearly differ between the two regions in which foxtail pine grows, influencing species, stand, and demographic characteristics. In the north, populations exist under a more mesic climatic regime, a diversity of geological substrates, stands of high tree species richness, lower densities and basal areas, but higher numbers of recruitment, with a relatively mixed size class distribution. Southern foxtail pine populations exist under a more xeric climatic regime dominated by granitic substrates, with moderate to high stand densities, less tree species-rich, lower recruitment numbers, but higher basal areas; largely due to a skewed size class distribution with high representation of large diameter trees.

Fecundity, a key demographic parameter in forest tree populations (see Clark et al. 1999), in this study was a function of the number of cones produced in a population and the number of recruits successfully established. At the stand or population-level, solar radiation input and foxtail pine density were correlated with fecundity across all locations, north and south. These factors may correspond with microenvironmental and topographic conditions that favor germination (e.g., warmer microclimate) in subalpine environments as well as propagule pressure (e.g., seed supply), which increases with tree size (basal area). Large-scale phenomena such as regional climate and landscape features are known to influence recruitment in subalpine forests (Millar et al. 2004, 2006; Bunn et al. 2005). But at the plot-level, microenvironmental conditions (e.g., litter, substrate type, and microhabitat) and factors corresponding to local seed supply (e.g., density, basal area, number of cones, and number of reproductive adults) may be equally as important to successful recruitment of foxtail pine.

An important limitation of this study is a lack of information about seed dispersal or seed/cone predation, both important factors in recruitment dynamics. Wind is the primary dispersal mechanism of foxtail pine seed (see Mastrogiuseppe and Mastrogiuseppe 1980). However, the presence of Clark's nutcracker in all the southern Sierra Nevada populations, even in the absence of whitebark pine, raises the question of the role of bird and/or small mammal dispersal. Clark's nutcrackers were observed in one of three sites in the Klamath region but this bird has been observed feeding on foxtail pine seed in this region, in sites where whitebark pine is not present (A. Eckert, Virginia Commonwealth Univ., personal communication). The closely-related Great Basin bristlecone pine (*P. longaeva*) resides in nearby mountain ranges (White, Inyo, and Panamint) to the east of foxtail pine in the southern Sierra Nevada. While Great Basin bristlecone pine is mainly dispersed by wind, Lanner (1988) and Lanner et al. (1984) have shown that Clark's nutcrackers can also play a role in dispersal and subsequent regeneration of this enigmatic high-elevation white pine. Seventy-eight percent of foxtail pine recruits in the southern Sierra Nevada were growing in a rock shelter (Table 4). While soil moisture availability and shade provided by a rock shelter can favor seed germination and seedling survival, Clark's nutcrackers are also known to select cache sites next to rocks (Tomback 1978). Another important factor influencing recruitment may be insect predation of cones and seed, which has been largely overlooked, but may have an overwhelming effect on cone production and seed supply in some years. In 2009 and 2010 a high frequency of insects (e.g., *Dioryctria* spp.) were observed in cones of foxtail pine in the southern Sierra

Nevada and Klamath region (D. Davis, A. Delfino Mix, P. Maloney, and D. Welty, personal observations). Both dispersal dynamics and cone/seed predation are areas in recruitment studies of forest trees that warrant further investigations.

Recruitment patterns of foxtail pine appear to be episodic in nature and other studies have observed this temporal trend for foxtail pine and other subalpine conifers (Millar et al. 2004, 2006; Bunn et al. 2005). Unfortunately this study lacks yearly temperature and precipitation data for these two regions that might be associated with recruitment years. Warmer temperatures and above average precipitation years can influence recruitment pulses (Millar et al. 2004, 2006; Bunn et al. 2005) and possibly the episodic recruitment patterns observed in this study.

Foxtail pine is recruiting in relatively higher numbers in the north than in the southern Sierra Nevada. But despite lower numbers of observed recruitment in some locations, most populations (north and south) appear to be buffered from declines due to high survivorship across all size classes, including larger reproductive individuals. Four of the six populations, two in the north and two in the south, appear to be stable, due to low mortality and high survival. Lake Mountain (λ = 0.998) and Sirretta Peak (λ = 1.007) have low estimated growth rates, due to low survivorship of individuals in the largest size class (0.786 and 0.762, respectively). The incidence of MPB was much higher and more frequently observed in the southern Sierra Nevada than in northern stands. Drought conditions appear to trigger MPB activity in the high elevation white pine forests of California (CFPC Reports 1976–2009; Millar et al. 2007). Because little is known about MPB in high elevation forests of California or about historical outbreaks, it is difficult to say what might be out of the range of historical variability for this native insect. Certainly old dead snags are observed in these forests but the causes of death are unknown. MPB-mediated mortality coupled with drought stress may be important factors contributing to current population trends at Lake Mountain and Sirretta Peak. Interestingly each of these populations represents the northern range limit (Lake Mountain) and southern range limit (Sirretta Peak) for the two subspecies in northwestern California and the southern Sierra Nevada, respectively (see Fig. 1).

The presence of WPBR at Lake Mountain may also be a predisposing factor influencing survivorship. In California, WPBR has only been found in northern foxtail pine stands and has not been confirmed in the southern stands of foxtail pine (Maloney, 2011). Latitudinal trends in WPBR incidence may correspond with a longer residence time for *C. ribicola* in the north (1929–1938) compared to the southern Sierra Nevada (1961) (Smith 1996). Climatic conditions in northern stands of foxtail pine are more favorable for *C. ribicola* infection (e.g., higher annual rainfall, warmer temperatures, and higher relative humidity), whereas the environment of the southern subspecies is drier and colder. We know that WPBR is present lower in elevation in Sequoia and Kings Canyon NP and Sequoia NF, but given the environment of the high Sierra Nevada where foxtail pine grows, these conditions may limit *C. ribicola* spread into these high elevation forests (see Maloney 2011).

Because population growth, λ, was calculated from a one-time sampling, our estimates may not reflect intrinsic variation in rates of fecundity, survivorship, mortality, and growth. Year to year variation in climate, cone production, cone and seed predation, recruitment success, tree mortality, insect dynamics, fire activity, and conditions favorable for WPBR infection can be considerable. Our intent was not to predict future population growth but to describe current population conditions and trends. Another limitation of our study is that the confidence intervals are very large for λ, which is a cause for concern, but it is difficult to assess the magnitude of this concern as λ was estimated from a one-time sampling that likely resulted in the large variances around the point estimate. Obtaining long-term demographic data for long-lived tree species is difficult, but will be critical to accurately access population dynamics of foxtail pine in an era of rapidly changing climate and increasing environmental stressors (e.g., insect outbreaks and non-native diseases). Ecological and environmental differences between the northern and southern subspecies may influence how *P. balfouriana* responds to natural and anthropogenic disturbances. Such information is basic to developing conservation, monitoring, and management strategies for this endemic and narrowly distributed white pine in subalpine forests of California.

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Appendix 1

Size-based transition matrices for recruitment (<1.37 meters in height) and stem diameters at breast height (1.37 m) in centimeters for six foxtail pine populations in California. Transition probabilities for survivorship and growth are in bold and shaded cells, respectively. Fecundity estimates are in italics.

Size description	Size n + t	Size year n					
		1	2	3	4	5	6
Lake Mountain, n = 153							
recruitment	1	**0.992**	0	0	*0.018*	*0.206*	*0.475*
0.1–5.0 dbh	2	0.008	**0.994**	0	0	0	0
5.1–10.0 dbh	3	0	0.006	**0.833**	0	0	0
10.1–20.0 dbh	4	0	0	0.056	**0.947**	0	0
20.1–40 dbh	5	0	0	0	0.053	**0.833**	0
≥40.1 dbh	6	0	0	0	0	0.006	**0.786**
Mount Eddy, n = 466							
recruitment	1	**0.999**	0	0	*0.034*	*0.658*	*1.338*
0.1–5.0 dbh	2	0.027	**0.995**	0	0	0	0
5.1–10.0 dbh	3	0	0.005	**0.993**	0	0	0
10.1–20.0 dbh	4	0	0	0.007	**0.988**	0	0
20.1–40 dbh	5	0	0	0	0.013	**0.917**	0
≥40.1 dbh	6	0	0	0	0	0.008	**0.934**
North Yolla Bolly, n = 141							
recruitment	1	**0.990**	0	0	*0.056*	*0.111*	*0.458*
0.1–5.0 dbh	2	0.010	**0.989**	0	0	0	0
5.1–10.0 dbh	3	0	0.100	**0.900**	0	0	0
10.1–20.0 dbh	4	0	0	0.100	**0.988**	0	0
20.1–40 dbh	5	0	0	0	0.013	**0.996**	0
≥40.1 dbh	6	0	0	0	0	0.042	**0.994**
Onion Valley, n = 154							
recruitment	1	**0.988**	0	0	*0.071*	*0.079*	*0.096*
0.1–5.0 dbh	2	0.013	**0.990**	0	0	0	0
5.1–10.0 dbh	3	0	0.100	**0.986**	0	0	0
10.1–20.0 dbh	4	0	0	0.014	**0.909**	0	0
20.1–40 dbh	5	0	0	0	0.045	**0.972**	0
≥40.1 dbh	6	0	0	0	0	0.028	**0.952**
Cottonwood Pass, n = 453							
recruitment	1	**0.998**	0	0	*0.063*	*0.218*	*0.445*
0.1–5.0 dbh	2	0.002	**0.998**	0	0	0	0
5.1–10.0 dbh	3	0	0.020	**0.995**	0	0	0
10.1–20.0 dbh	4	0	0	0.045	**0.903**	0	0
20.1–40 dbh	5	0	0	0	0.032	**0.905**	0
≥40.1 dbh	6	0	0	0	0	0.024	**0.902**
Sirretta Peak, n = 54							
recruitment	1	**0.900**	0	0	*0.008*	*0.024*	*0.046*
0.1–5.0 dbh	2	0.100	**0.900**	0	0	0	0
5.1–10.0 dbh	3	0	0.100	**0.900**	0	0	0
10.1–20.0 dbh	4	0	0	0.100	**0.983**	0	0
20.1–40 dbh	5	0	0	0	0.017	**0.988**	0
≥40.1 dbh	6	0	0	0	0	0.013	**0.762**